

Early Life History of the Giant Clams *Tridacna crocea* Lamarck, *Tridacna maxima* (Röding), and *Hippopus hippopus* (Linnaeus)¹

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ABSTRACT: Giant clams may be stimulated to spawn by the addition of macerated gonads to the water. Individuals of *Tridacna maxima* collected at Anae Island, Guam, spawned from November to March. On Palau, *Hippopus hippopus* spawned in June and *Tridacna crocea*, in July.

Tridacna crocea, *T. maxima*, and *H. hippopus* displayed a stereotyped development pattern in morphogenesis and rate of development. Fertilized eggs of *T. crocea*, *T. maxima*, and *H. hippopus* had mean diameters of 93.1, 104.5, and 130.0 μm , respectively. The day-2 straight-hinge veligers of *T. crocea*, *T. maxima*, and *H. hippopus* had mean shell lengths of 155.0, 168.0, and 174.4 μm , respectively. Settlement occurred 12, 11, and 9 days after fertilization at a mean shell length of 168.0, 195.0, and 202.0 μm for *T. crocea*, *T. maxima*, and *H. hippopus*, respectively. Metamorphosis was basically complete about 1 day after settlement. Juveniles of *T. crocea*, *T. maxima*, and *H. hippopus* first acquire zooxanthellae after 19, 21, and 25 days, respectively. Growth rates increase sharply after the acquisition of zooxanthellae. Juvenile shells show first signs of becoming opaque after 47 days for *T. maxima* and after 50 days for *H. hippopus*.

GIANT CLAMS are protandric functional hermaphrodites (Wada 1942, 1952). The male phase of the gonad develops first and then the female phase. In the adults, female and male follicles lie side by side throughout the extent of the gonad, and both eggs and sperm mature simultaneously.

The giant clams, in contrast to the majority of functional hermaphrodite bivalves, do not discharge eggs and sperm simultaneously when spawning. Giant clams first spawn sperm and then eggs. The spawning reaction has been described by Wada (1954). Stephenson (1934), in her work with *Hippopus hippopus*, provided useful information for judging the gonad condition of giant clams.

LaBarbera (1974) described the transitional stage between the trochophore and the veliger larva of *Tridacna squamosa*, prodissoconch I shell

formation, and initial organogenesis. The larval and postlarval development of *Tridacna maxima* and *T. squamosa* have been described by LaBarbera (1975) in his efforts to understand the mode of transmission of zooxanthellae from generation to generation and to elucidate the mechanism of development and possible evolution of the unique form of tridacnids.

The motive behind investigating the early life history of the giant clam is twofold. First, giant clams are being subjected to an ever-increasing fishing pressure because of their food and shell value. Data about the early life history of the clam might alleviate some of this pressure by providing conservationists with the information they need to support efficient population management. Second we must obtain a basic knowledge of the early life history of the giant clam before we can determine the feasibility of a large-scale aquaculture of the animal for food.

On Guam, research was conducted on *T. maxima* at the University of Guam Marine Laboratory from September 1973 to March 1975. Research was carried out on *Tridacna crocea*, *Tridacna derasa*, *Tridacna gigas*, and *H. hippopus* in Palau at the Micronesian Mari-

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culture Demonstration Center (MMDC) from 7 June to 19 August 1974.

MATERIAL AND METHODS

On Guam, specimens of *Tridacna maxima* were collected exclusively at Anae Island at depths of 3–10 meters. Because this species is usually found embedded in the substrate, I removed it by chipping away the surrounding substrate with a hammer and chisel, and then by cutting the byssus clean with a thin-bladed filet knife. This method was preferred as it did not injure the animal.

Specimens of *H. hippopus* and *T. derasa* were collected in Palau at Ngarchabal Island at depths of 6–10 meters. Specimens of *T. crocea* were collected from the reef at the MMDC dock at a depth of 1–4 meters, with the same methods being used as described for *T. maxima*. Specimens of *T. gigas* were collected at a depth of about 3 meters near the Malakal Passage lighthouse; here a rope sling was attached to the clam and the animal was hoisted to the bottom of the boat. Then, with the boat being run at slow speed, the clams were towed underwater to MMDC.

Four to 12 individuals of *T. maxima* were collected monthly at Anae Island, Guam, from November 1973 to March 1975, except for the months of December 1973, and October 1974. They were subjected to spawning stimulus (macerated gonad) the day after collection. If no eggs were spawned, the animals were dissected and the gonads were inspected microscopically. In spawning experiments only clams greater than 130 mm in shell length were used, as *T. maxima* does not attain full sexual maturity, i.e., develop the female phase, until it attains a shell length of 110–130 mm. Gonad specimens were preserved in 70 percent isopropyl alcohol.

The fecundity of *T. maxima* was estimated from eight clams collected during February 1975. The number of eggs spawned by each of the individuals in separate containers was counted by volumetric estimate. Five to 10 ml of macerated gonad was used to stimulate these clams to spawn. They were allowed to spawn until the water was very dense with sperm. The clams were transferred repeatedly to new containers until they spawned eggs. Five to 10 ml

of seawater containing sperm were added to the container to fertilize the eggs. A net system of a 210- μ m nylon mesh over an 88- μ m nylon mesh was used to isolate the eggs. Large detritus was caught on the top net, eggs were caught on the bottom net, and sperm and water passed through both nets. The eggs from the bottom net were gently washed into a 5-liter glass container containing filtered seawater. The number of eggs was then adjusted so that only one layer of eggs covered the bottom after settling had occurred. A settling and decanting technique was used to wash the eggs three times, after which they were placed in several 500-liter tanks at a concentration of about 10,000 eggs per tank. A prolonged washing period decreases survival, so fertilized eggs were washed only three times before being placed in a large tank. The 500-liter holding tanks contained seawater that had been filtered through an 88- μ m nylon mesh that removed large detritus and potential predators. Larval and juvenile *T. maxima* were raised in the 500-liter rearing tanks. No additional nutrients were added to those present naturally in the seawater. The water in the rearing tanks for juveniles was changed once a week.

Complete spawning was also stimulated when 22 *T. maxima* were transferred from a 500-liter holding tank at 26.1° C to a 1000-liter holding tank that was being filled. Initially, the holding tank had only 6 inches of water in it. As more water was added, a circular flow developed in the tank. The water being added was at 29.7° C. Once the tank had been filled, the water cooled to 28.5° C and several clams spawned.

To test substrate preference, I used various substrates (bare rock, rocks covered with coral-line algae, glass, shells, and dead coral) as spat collectors during the settlement of *T. maxima*. Substrates were suspended in the tanks from a series of monofilament slings attached to sticks that had been placed across the tops of the rearing tanks.

On Palau, suspended glass petri dishes, some with a sand bottom and others without, were used as spat collectors for *H. hippopus*. Suspended glass petri dishes, some with a sand bottom and others with an assorted dead coral bottom, were used as spat collectors for *T. crocea*.

TABLE 1
MONTHLY DATA ON GONAD CONDITION OF A POPULATION OF *Tridacna maxima*,
ANAE ISLAND, GUAM

GONAD CONDITION	1973				1974												1975	
	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB		
Ripe	1	-	3	8	-	-	-	-	-	-	-	-	-	3	-	7		
9/10 Ripe	3	-	-	1	-	2	2	-	1	3	1	-	-	1	1	-		
7/10 Ripe	1	-	-	-	-	2	3	1	2	2	-	-	-	1	3	-		
1/2 Ripe	3	-	1	-	3	3	2	4	3	-	-	-	1	1	1	-		
Spent	4	-	-	-	2	-	-	-	-	-	5	-	3	-	1	-		

NOTE: Ripe, spawned eggs after stimulus; 9/10 Ripe, egg size from 100–150 μm , gonad very large, white; 7/10 Ripe, egg size from 80–150 μm , gonad large, white; 1/2 Ripe, egg size from 50–150 μm , gonad small, white; Spent, very few to no eggs present, gonad small, brown to olive drab.

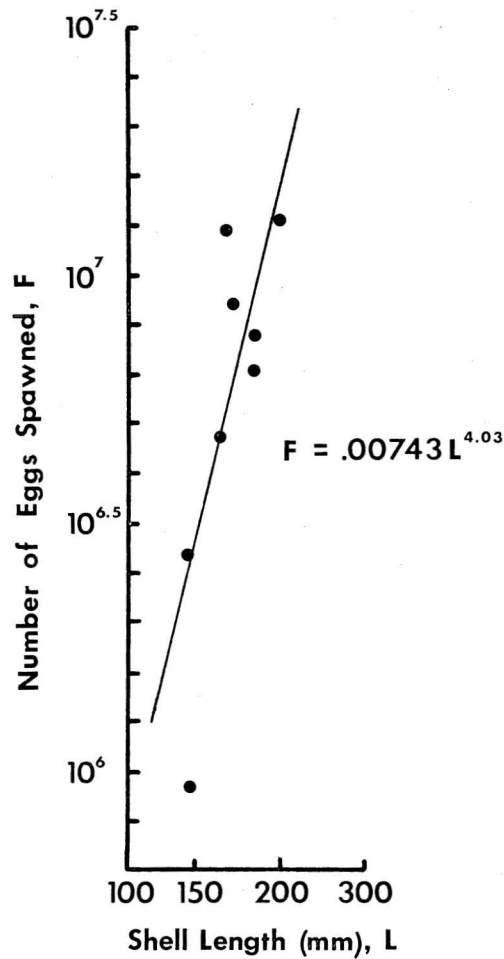


FIGURE 1. Logarithmic plot of numbers of eggs spawned in relation to shell length of *Tridacna maxima* at Anae Island, Guam.

After settlement, some juveniles of *T. crocea* and *H. hippopus* that had settled on petri dishes were placed in a 6 \times 4 \times 2 foot canvas swimming pool with a running seawater flow, and others were left in the rearing tanks. The water in the rearing tanks was changed every 2 days.

RESULTS

Spawning and Gonad Condition

After the macerated gonad had been added to the water, the clams would usually spawn sperm within 2 to 3 minutes. They continued to spawn sperm for as long as 6 hours or more, with individuals exhibiting variation in duration. After the spawning of sperm, the spawning of eggs will proceed if the gonad is fully ripe. If the gonad is not fully ripe, only the spawning of sperm will occur.

The results from monitoring the gonad condition of *T. maxima* at Anae Island are given in Table 1. Field-collected animals stimulated by macerated gonad spawned eggs in November 1973; in January, February, and December 1974; and in February 1975. During no other months could *T. maxima* at Anae Island be stimulated to spawn eggs. Spent gonads were found in dissected specimens during the months of November 1973; March, September, and November 1974; and January 1975. From April through August, specimens in varying degrees of ripeness were observed.

The number of eggs spawned by *T. maxima*

TABLE 2

EARLY LIFE CHRONOLOGY OF THE GIANT CLAMS *Tridacna crocea*, *Tridacna maxima*,
AND *Hippopus hippopus*

ITEM	<i>T. crocea</i>	<i>T. maxima</i>	<i>H. hippopus</i>
Culture Temperature Range	27.5°–35.1° C	26.0°–29.8° C	27.5°–35.1° C
1st Cleavage	50 min	60 min	55 min
Ciliated Gastrula	7 hr	7 hr	8 hr
Trochophore	15 hr	16 hr	17 hr
Straight-Hinge Veliger	20 hr	20 hr	24 hr
Pediveliger	10 (9–17) days	9 (8–19) days	7 (6–15) days
Settlement	12 (11–17) days	11 (10–19) days	9 (8–15) days
Metamorphosis	13 (12–18) days	12 (11–20) days	10 (9–16) days
1st Juvenile with Zooxanthellae	19 days—190 μ m	21 days—250 μ m	25 days—230 μ m
Smallest Juvenile with Zooxanthellae	190 μ m—19 days	210 μ m—26 days	200 μ m—27 days
1st Opaque Juvenile	—	47 days—440 μ m	50 days—435 μ m
Smallest Opaque Juvenile	—	440 μ m—47 days	435 μ m—50 days

NOTE: Numerals in parentheses represent ranges. All times after first cleavage have been rounded off to the nearest hour; all times mentioned begin at time of fertilization. The times listed for development, unless otherwise specified, represent the point at which approximately 50 percent of the individuals observed from the cultures had reached that stage.

varied with the size of the individual (Figure 1) and can be expressed by the equation

$$F = 0.00743L^{4.03},$$

where F is the number of eggs spawned and L is the shell length.

Hippopus hippopus spawned sperm and eggs on 12 June in Palau. A clam 249 mm in length spawned approximately 25 million eggs. Later in August a *H. hippopus* 280 mm in length was dissected and found to be in a halfripe condition. *Tridacna crocea* spawned sperm and eggs on 7 July. However, more than 30 clams were subjected to spawning stimulus before 2 finally spawned eggs.

Specimens of *T. derasa* 390 and 410 mm in shell length were subjected to spawning stimulus on 3 July 1974 and no spawning occurred. The specimens were then dissected and were found to be spent. Two *T. gigas* 530 and 560 mm in shell length were found on 26 July 1976 to be still in the male phase.

Early Life Chronology

The early life chronologies of *T. crocea*, *T. maxima*, and *H. hippopus* are presented in Table 2. *Tridacna maxima* was cultured on four different occasions, with fertilization occurring 12 November 1973; and 31 January, 14 Febru-

ary, and 22 February 1974. The early life chronology is a composite of the above cultures.

Tridacna crocea, *T. maxima*, and *H. hippopus* displayed a stereotyped development pattern (Figures 2, 3, 4) that is considered to be typical for bivalves in general. Development times and sizes at a particular stage exhibit much individual variation (Tables 2, 3, 4, 5). In general, the three species observed exhibited similar development times, if the great range of individual variation in these times is considered.

Larval Development and Behavior

After fertilization, typical bivalve spiral cleavage results in a spherical blastula. The rotating ciliated gastrulae may be observed 7 hours after fertilization for *T. crocea* and *T. maxima* and after 8 hours for *H. hippopus*.

Pelagic larvae exhibit typical bivalve development and behavior (D'Asaro 1967, Loosanoff and Davis 1963, Raven 1958) with the following specific variations. The trochophore stage (Figures 2a, 4a) is reached for *T. crocea*, *T. maxima*, and *H. hippopus* 15, 16, and 17 hours after fertilization, respectively. The transitional stage between the trochophore and the veliger larva (Figure 4b) has been described by La-Barbera (1974).

Straight-hinge veligers (Figures 2b, 3a, 4c)

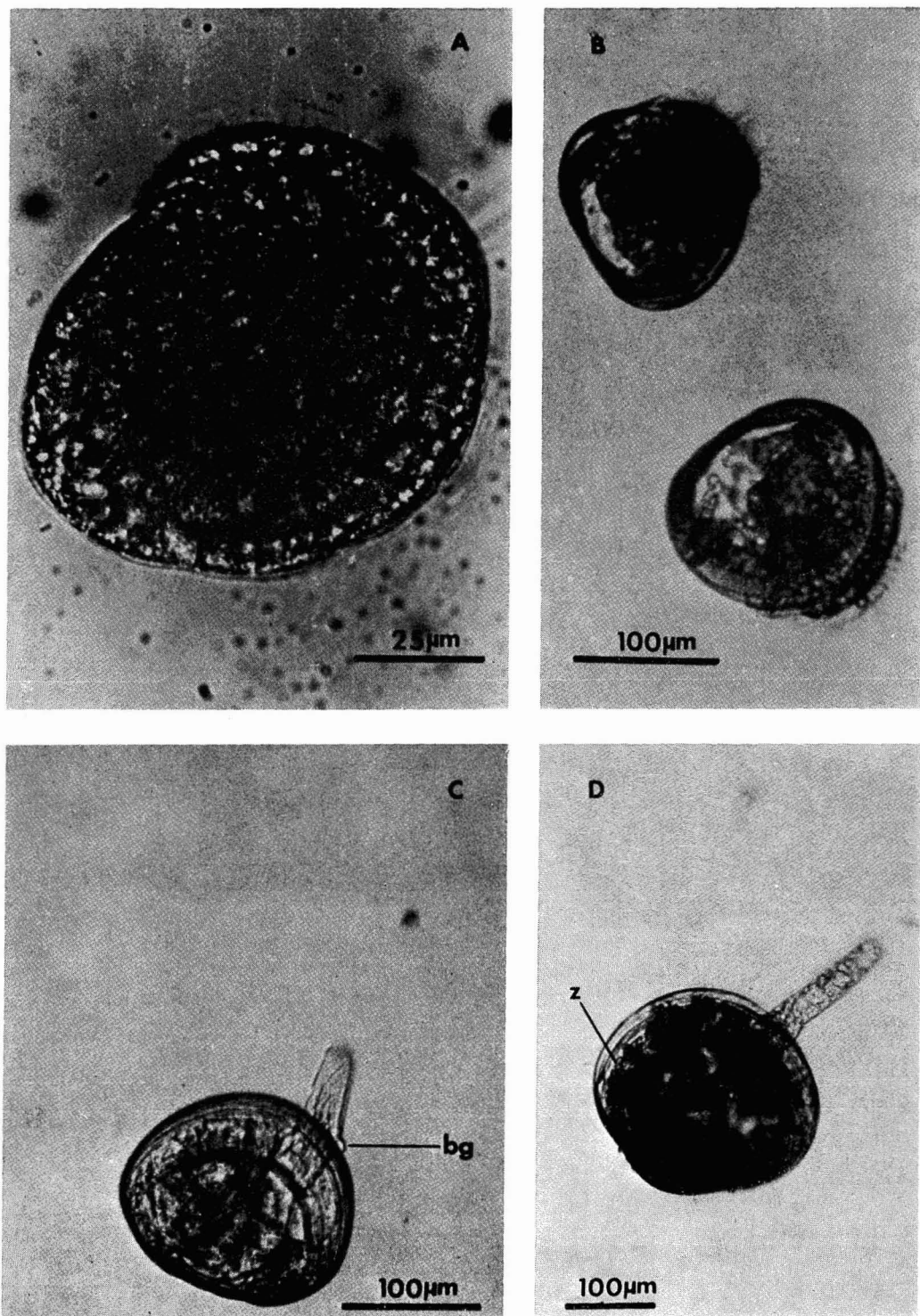


FIGURE 2. Larval and juvenile *Tridacna crocea*. A, trochophore; B, day-3 veligers; C, day-10 pediveliger; D, day-25 juvenile.

ABBREVIATIONS: bg, byssus gland; z, zooxanthellae.

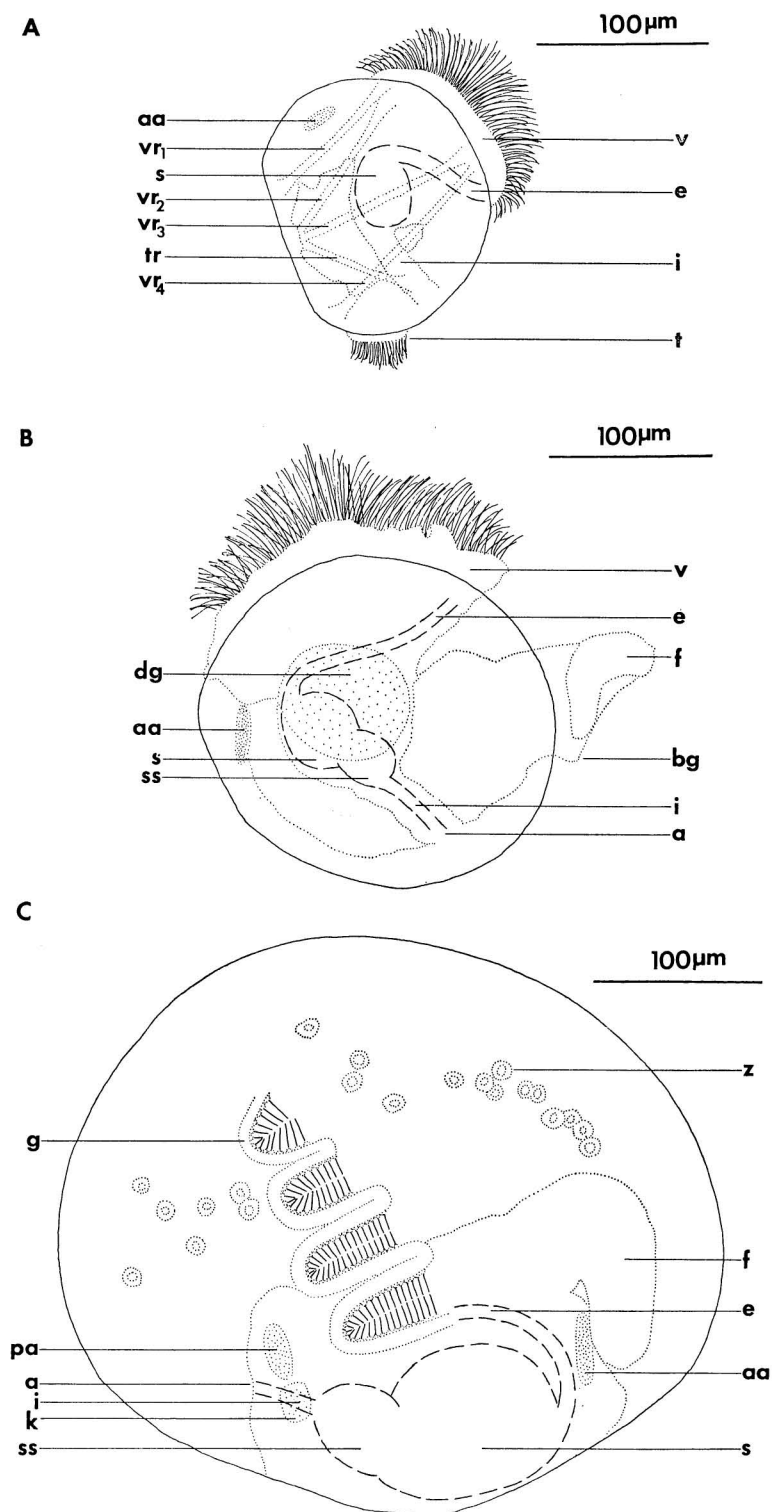


FIGURE 3. Internal anatomy of larval and postlarval *Tridacna maxima*. A, day-2 veliger; B, pediveliger; C, day-47 juvenile.

ABBREVIATIONS: a, anus; aa, anterior adductor; bg, byssus gland; dg, digestive gland; e, esophagus; f, foot; g, gill; i, intestine; k, kidney; pa, posterior adductor; s, stomach; ss, style sac; t, telotroch; tr, telotrochal retractor; v, velum; vr, velar retractors (numbered); z, zooxanthellae.

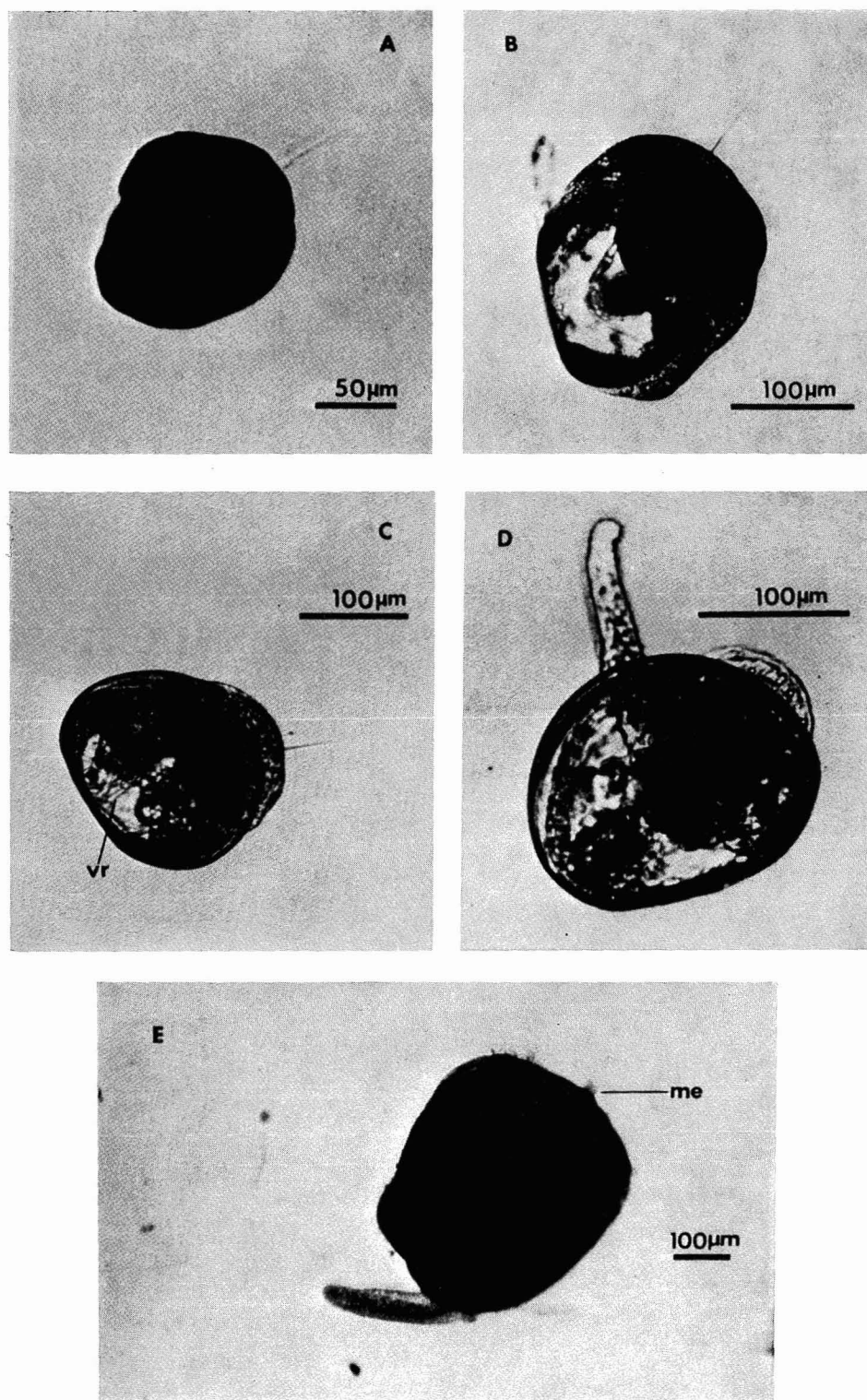


FIGURE 4. Larval and juvenile *Hippopus hippopus*. A, trochophore; B, trochophore-veliger transition stage; C, day-4 veliger; D, day-11 pediveliger; E, day-58 juvenile.

ABBREVIATIONS: me, mantle extension; vr, velar retractor.

TABLE 3

GROWTH IN LENGTH AND HEIGHT BY TIME FOR *Tridacna crocea*

STAGE	TIME	NUMBER	LENGTH (μm)	HEIGHT (μm)
Fertilized Eggs	0	8	93.1 \pm 3.2 (90-97)	
Straight-Hinge Veliger	day-2	7	155.0 \pm 4.1 (150-160)	130.0 \pm 4.1 (125-135)
Straight-Hinge Length	day-2	5	85.0 \pm 5.0 (80-90)	
Pediveliger	day-10	5	173.0 \pm 2.7 (170-175)	
Settlement	day-12	5	168.0 \pm 2.7 (165-170)	146.0 \pm 4.2 (140-150)
Juvenile	day-17	5	182.0 \pm 5.7 (175-190)	
Juvenile	day-25	9	201.7 \pm 29.4 (165-260)	
Juvenile	day-35	3	228.3 \pm 62.5 (185-300)	

NOTE: Numerals in parentheses following standard deviations represent ranges.

TABLE 4

GROWTH IN LENGTH AND HEIGHT BY TIME FOR *Tridacna maxima*

STAGE	TIME	NUMBER	LENGTH (μm)	HEIGHT (μm)
Fertilized Eggs	0	10	104.5 \pm 5.5 (100-115)	
Straight-Hinge Veliger	day-2	5	168.0 \pm 4.5 (160-170)	140.0 \pm 0 (140-140)
Straight-Hinge Length	day-2	4	91.3 \pm 2.5 (90-95)	
Veliger	day-4	8	178.8 \pm 5.2 (170-185)	
Veliger	day-6	6	184.2 \pm 4.9 (180-190)	
Pediveliger	day-9	7	192.1 \pm 9.1 (180-200)	
Settlement	day-11	7	195.0 \pm 8.7 (180-205)	168.5 \pm 2.8 (160-180)
Juvenile	day-14	11	203.0 \pm 5.3 (200-215)	
Juvenile	day-16	4	237.5 \pm 43.3 (200-300)	
Juvenile	day-24	8	258.7 \pm 34.5 (200-325)	
Juvenile	day-40	5	264.0 \pm 53.2 (220-350)	
Juvenile	day-47	6	444.2 \pm 106.4 (280-550)	
Juvenile	day-64	5	673.0 \pm 96.2 (565-800)	
Juvenile	day-72	3	745.0 \pm 101.5 (635-835)	
Juvenile	day-91	8	617.5 \pm 191.1 (400-835)	

NOTE: Numerals in parentheses following standard deviations represent ranges.

TABLE 5

GROWTH IN LENGTH AND HEIGHT BY TIME FOR *Hippopus hippopus*

STAGE	TIME	NUMBER	LENGTH (μm)	HEIGHT (μm)
Fertilized Eggs	0	6	130.0 \pm 6.3 (120-140)	
Straight-Hinge Veliger	day-2	9	174.4 \pm 12.4 (150-190)	146.6 \pm 7.1 (130-150)
Straight-Hinge Length	day-2	5	108.0 \pm 8.4 (100-120)	
Veliger	day-3	6	191.6 \pm 4.1 (190-200)	
Pediveliger	day-7	5	200.0 \pm 0 (200-200)	
Settlement	day-9	5	202.0 \pm 2.7 (200-205)	166.0 \pm 2.2 (165-170)
Juvenile	day-14	5	200.0 \pm 3.5 (195-205)	
Juvenile	day-20	12	216.6 \pm 10.5 (205-240)	
Juvenile	day-27	6	219.1 \pm 17.7 (200-235)	
Juvenile	day-38	3	288.3 \pm 48.6 (235-330)	
Juvenile	day-50	6	391.6 \pm 68.5 (300-500)	
Juvenile	day-58	9	666.1 \pm 89.6 (535-835)	

NOTE: Numerals in parentheses following standard deviations represent ranges.

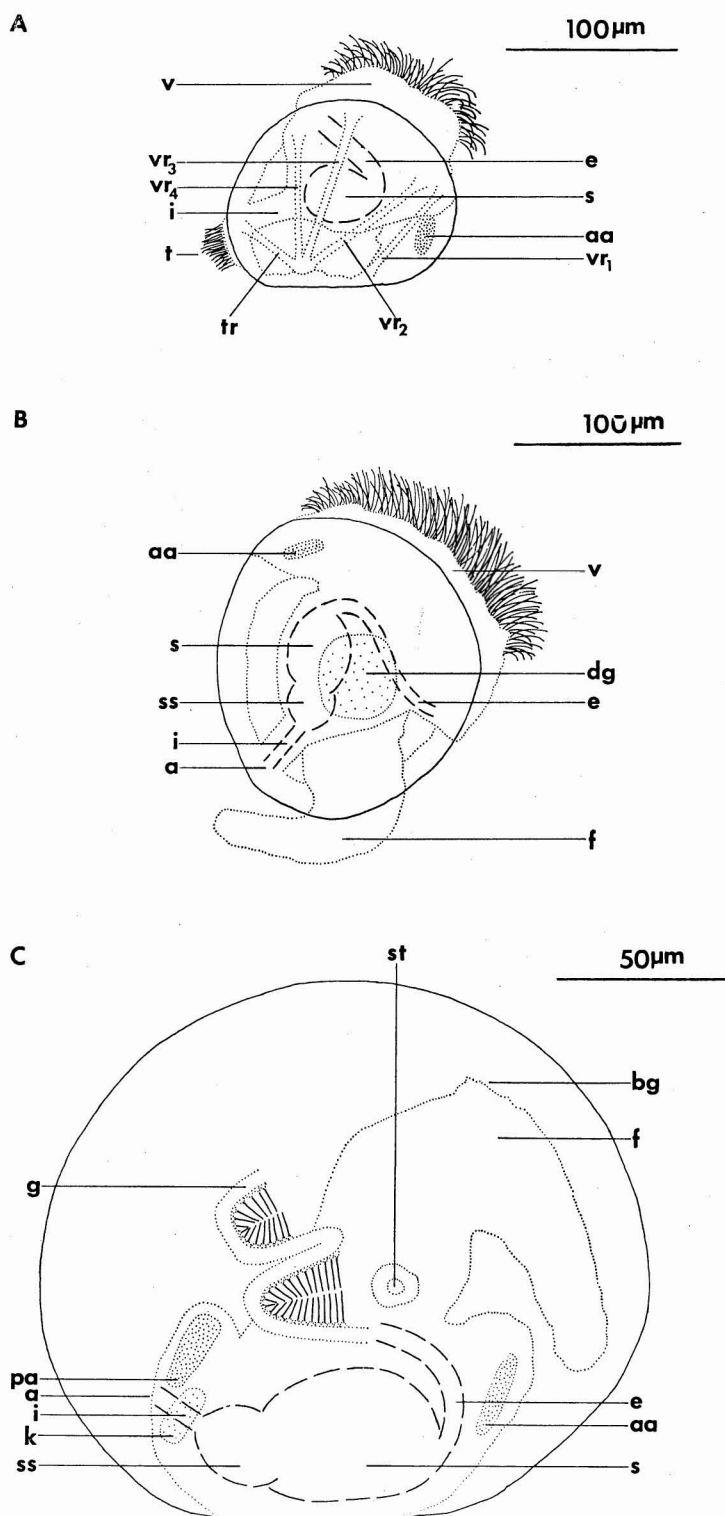


FIGURE 5. Internal anatomy of larval and postlarval *Tridacna crocea*. A, day-2 veliger; B, pediveliger; C, day-25 juvenile.

ABBREVIATIONS: a, anus; aa, anterior adductor; bg, byssus gland; dg, digestive gland; e, esophagus; f, foot; g, gill; i, intestine; k, kidney; pa, posterior adductor; s, stomach; ss, style sac; st, statocyst; t, telotroch; tr, telotrochal retractor; v, velum; vr, velar retractors (numbered).

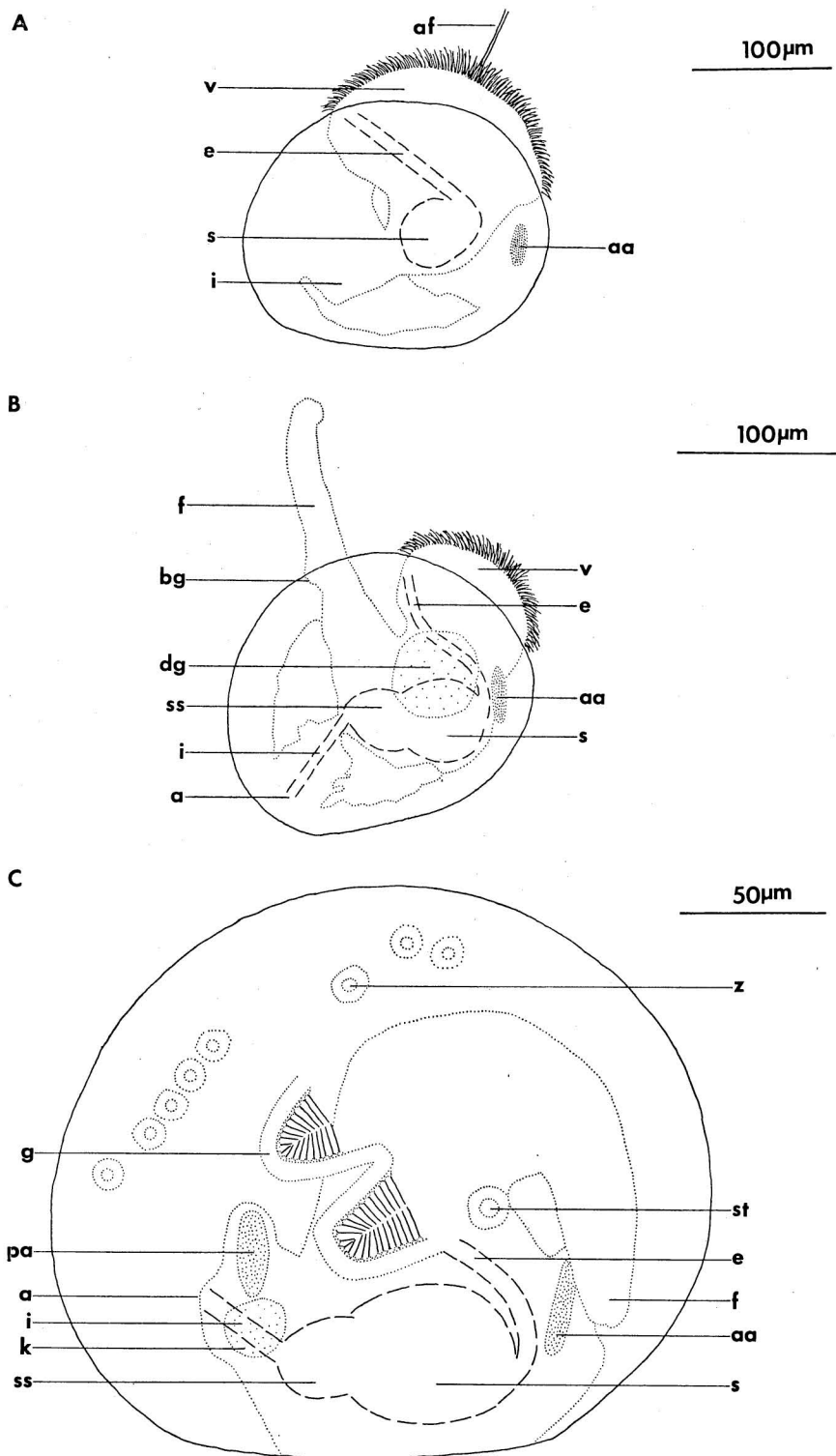


FIGURE 6. Internal anatomy of larval and postlarval *Hippopus hippopus*. A, day-2 veliger (see Figure 4C for arrangement of retractor muscles); B, pediveliger; C, day-27 juvenile.

ABBREVIATIONS: a, anus; aa, anterior adductor; af, apical flagella; bg, byssus gland; dg, digestive gland; e, esophagus; f, foot; g, gill; i, intestine; k, kidney; pa, posterior adductor; s, stomach; ss, style sac; st, statocyst; v, vellum; z, zooxanthellae.

have their own characteristic arrangement of retractor muscles (Figures 3a, 4c, 5a). *Tridacna squamosa* raised by LaBarbera (1975) had the same basic arrangement of retractor muscles as does *T. crocea*. The day-2 prodissoconch I (PD-I) shell of *T. crocea* and *T. maxima* are similar in shape. The day-2 PD-I shell of *H. hippopus* has a less steeply sloping posterior shoulder than do those of *T. crocea* and *T. maxima* (Figures 3a, 5a, 6a). By day-3 the intestine becomes hollow and the straight-hinge veligers actively feed. Food is kept in motion by cilia in the stomach. At all times the digestive gland is either dark brown or gold. All three species feed primarily on a flagellate which is round in shape and about 5 μ m in diameter.

Pediveligers (Figures 3b, 5b, 6b) have developed for *T. crocea*, *T. maxima*, and *H. hippopus* by days 10, 9, and 7, respectively. The shell has begun to lose its definite straight-hinge appearance because of the slight growth of the umbo (Figures 2c, 3b, 4d), and has increased in length. The stomach is now two-chambered, with a slight constriction separating the style sac from the anterior stomach chamber. The anterior stomach chamber is less ciliated than is the posterior style sac. The esophagus opens into the stomach and has decreased in diameter. The stomach chamber also has openings coming from the digestive gland and an opening to the style sac. Cilia are present at the tip of the foot and smaller cilia run down the length of the foot to the byssus gland. Pediveligers alternately swim about and crawl on the bottom. Crawling is accomplished by attaching the tip of the foot to the substrate and then pulling the rest of the body forward. Another form of locomotion is a gliding movement which is accomplished by the animal's extending the foot and using the cilia on the tip of the foot to produce a gliding effect or continuous pull. A more bizarre form of locomotion was exhibited by a young juvenile that was attached to a filamentous alga. After slight movement of the alga, the juvenile propelled itself through the water to another filament by rapidly contracting its valves. Upon arrival, the young clam, using its foot, immediately attached to the new filament. The foot is also used for testing and orientating the clam with the substrate.

Settlement and Metamorphosis

Settlement and metamorphosis are gradual processes. The appearance of an active foot signifies that the time for settlement is near and that metamorphosis is beginning. Pediveligers with a functional velum and foot alternately swim about and crawl on the bottom and possess a recently developed posterior adductor muscle and kidney. When swimming, most are confined to the lower half of the culture tank because of the increase in shell weight and reduction in size of the velum. After a period of alternately swimming, crawling, and making temporary attachments to the substrate, the pediveliger becomes increasingly sedentary in its habits. The velum gradually degenerates, confining the clam to the substrate while functional gills develop (Figures 3c, 5c, 6c). Also at this time, a statocyst located at the base of the foot (Figures 5c, 6c) was first observed in *T. crocea* and *H. hippopus*. Its presence basically indicates completion of metamorphosis. Settlement is 50 percent complete for *T. crocea*, *T. maxima*, and *H. hippopus* by days 12, 11, and 9, respectively. About 50 percent of the clams observed from culture had completed metamorphosis by days 13, 12, and 10 for *T. crocea*, *T. maxima*, and *H. hippopus*, respectively. The times of settlement and metamorphosis exhibit much individual variation (Table 2).

Juveniles demonstrate definite thigmotactic reactions and, after metamorphosis, continue to crawl until they find a suitable place to attach by means of the byssus gland. Experiments in which different substrates were used seem to indicate that juveniles prefer a permanent settling spot that can protect them from as many different angles as possible. For example, four crawling juveniles of *T. crocea* were introduced into a rectangular holding tank continually supplied with fresh seawater. The juveniles took, as their preference for permanent settling sites, the corners of the tank. Later, more juveniles were introduced. Since the corners were already filled, they took as their preference for permanent settling sites the edges of the tank. Apparently, maximum protection governs the choice of site of permanent settlement. This seems warranted, as smaller individuals appear to be more susceptible to predation in their early life.

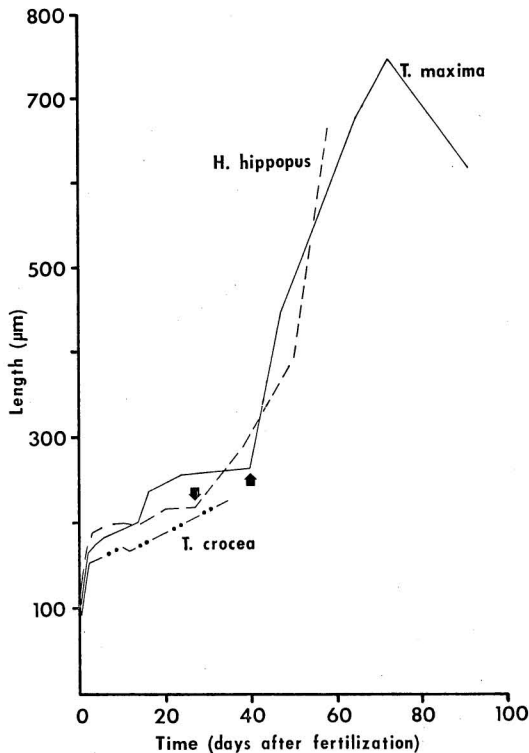


FIGURE 7. Growth in length of *Tridacna crocea*, *Tridacna maxima*, and *Hippopus hippopus*. For clarity, only mean values have been plotted. See Tables 3, 4, and 5 for ranges and standard deviations. Arrows indicate the time at which the majority of the culture had acquired zooxanthellae.

Preliminary experiments in which juveniles ranging in length from 600 μm to 3 cm were used demonstrated that only clams over 1 cm survived predation after being introduced into a natural situation.

Juvenile Development

The acquisition of zooxanthellae in the mantle of juvenile *T. crocea* (Figure 2d), *T. maxima*, and *H. hippopus* occurred between 19–25, 21–40, and 25–27 days, respectively. The smallest juvenile with zooxanthellae for *T. crocea*, *T. maxima*, and *H. hippopus* was 190, 210, and 200 μm in shell length, respectively. In general, the three species acquire zooxanthellae soon after metamorphosis. The shell of juveniles with zooxanthellae has a definite umbo (Figure 2d), least pronounced in *T. crocea*. The stomach,

which previously only contained small flagellates, now also has zooxanthellae rotating in it. The anterior and posterior adductor muscles are present.

Juvenile shells with opaque patches were observed for *T. maxima* on day-47 and for *H. hippopus*, on day-50. Juveniles without opaque patches could still be observed for *T. maxima* on day-91 and for *H. hippopus*, on day-58. The shell length of the smallest juvenile with first signs of opaque patches was 440 μm for *T. maxima* and 435 μm for *H. hippopus*. In general, the time and smallest size at which *T. maxima* and *H. hippopus* first show opaque patches are relatively similar. The majority of opaque patches are usually apparent first in the ventral region. However, minor patches in various other locations were also noticed. The shell of juveniles showing opaque patches is heart-shaped, and the mantle is packed with zooxanthellae (Figure 4e). Mantle extensions (Figure 4e), which have small terminal bristles and may be sensory in function, are also developed on *T. maxima* and *H. hippopus*. Labial palps are present and active. An extended exhalant siphon is evident in *T. maxima* at this time. The heart was first observed beating on day-47 in a specimen of *T. maxima* that had a shell length of 360 μm . The rate of heart beat is very irregular and ranges from 19 to 31 beats per minute.

Growth

Mean sizes in length, ranges, and standard deviations for the different stages of *T. crocea*, *T. maxima*, and *H. hippopus* are presented in Tables 3, 4, and 5. Mean length in relation to time for the three species is plotted in Figure 7 for comparison.

The growth (maximum linear dimension) curves for the three species exhibit similar basic characteristics. The growth rate of the veliger shell is low (1.2 $\mu\text{m}/\text{day}$ for *T. crocea*, 2.7 $\mu\text{m}/\text{day}$ for *T. maxima*, 3.5 $\mu\text{m}/\text{day}$ for *H. hippopus*). Shell growth rates after settlement and metamorphosis until day-35 for *T. crocea*, day-40 for *T. maxima*, and day-27 for *H. hippopus* are also low (2.5 $\mu\text{m}/\text{day}$ for *T. crocea*, 2.3 $\mu\text{m}/\text{day}$ for *T. maxima*, 0.9 $\mu\text{m}/\text{day}$ for *H. hippopus*). After day-40 (*T. maxima*) and day-27 (*H. hippopus*), growth

rate increases sharply ($6.8 \mu\text{m/day}$ for *T. maxima*, $13.9 \mu\text{m/day}$ for *H. hippopus*). This corresponds to the time at which the majority of juveniles had acquired zooxanthellae.

DISCUSSION

Observations of the gonad condition of a population of *T. maxima* at Anae Island indicated that the winter months of November to March are the most promising for spawning. The height of the spawning period seems to occur in February. It appears that the majority of the population is in the process of recovering from winter spawning between March and August. Some highly mature individuals were observed at this time and some spawning may occur but probably only to a small extent. Spawning seems to increase in frequency around August or September and to peak again in February.

Stephenson (1934) reported that *H. hippopus* spawns in the austral summer months of December to March on the reef flat at Low Isles, Great Barrier Reef. She suggested high temperatures during two hot spells as being the stimulus for spawning. The first hot spell occurred from 7 December to the end of the month, with temperatures ranging from 28.0° – 30.7° C. The second hot spell occurred from 12–30 January, with temperatures ranging from 29.0° – 32.0° C. Such hot spells may be a factor in stimulating spawning among reef-flat animals which are exposed to temperature fluctuations.

It is doubtful that temperature plays any role in the spawning period of *T. maxima* at Anae Island, because the annual temperature range for oceanic surface water around Guam is 26.5° – 29.0° C. Deeper waters have insignificant annual temperature fluctuations; giant clams living in deeper waters are probably influenced in their spawning activities by some other factor. Evidence suggests that temperature is not a factor in determining the spawning period of subtidal populations. Populations in relatively constant temperature environments may be genetically disposed to synchronize their spawning behavior to a characteristic environmental stimulus that may be unique to each population's location.

It is also interesting that *H. hippopus* spawned in the summer months in Australia and Palau; whereas *T. maxima* spawned during the winter months in Guam and Fiji (LaBarbera 1975). The same species may spawn during the same month of the year regardless of geographical location. Further investigation is needed into this question.

Many temperature-shifting experiments similar in style to those used in spawning temperate-water bivalves (Galtsoff 1938) were carried out, with various temperatures and different periods of exposure being used. None of these procedures stimulated spawning; in some cases they made the animal sick or even killed it. In the study of tropical bivalves one should consider the different environmental conditions to which tropical coral-reef organisms are exposed and not expect to find the same reproductive processes or strategies that are common to temperate water species.

Spawning in nature may be stimulated by water movement. Previous experiments designed to stimulate spawning by changing water temperature failed, but spawning was stimulated when clams were subjected to a current of circular flowing water in a holding tank that was being filled. In Guam, rougher than average sea states occur from September to January as a result of large swells generated by the trade winds, which are strongest at this time. At Anae Island continuous large swells that cause very strong currents underwater during one or several winter months are common. The coincidence of strong underwater currents during the spawning period at Anae Island may further support this idea. LaBarbera (1975) noted the apparent effects of the changing tide in stimulating the spawning of clams in Fiji.

Adding macerated gonad to seawater containing giant clams seems to be the easiest and most efficient way to stimulate spawning. Wada (1954) contended that the active principle that stimulates spawning comes from both the eggs and the primordial oogonia or other ovarian tissue cells. The active principle seems to be species-specific in effect, as *T. maxima* would not react to stimulation if *T. squamosa* eggs were used and vice versa (LaBarbera 1975), nor would *T. squamosa* react to stimulation if *H. hippopus* or *T. derasa* eggs were used, and *T. derasa* would

not react to stimulation if *T. squamosa* or *H. hippopus* eggs were used (Wada 1954).

When spawning giant clams for culture, one must ensure that the spawning of eggs occurs in seawater with a low density of sperm. Spawning eggs with an excess of sperm in the surrounding jellycoat do not develop normally. This problem was also observed by LaBarbera (1975).

The pelagic larval period of the three species observed is short (12 days for *T. crocea*, 11 days for *T. maxima*, 9 days for *H. hippopus*), and under better culture conditions could probably be shortened further. LaBarbera (1975) also observed similar short pelagic periods when culturing *T. maxima* and *T. squamosa* in Fiji.

Larvae can be cultured adequately in a stagnant system but a food supplement and bacteriostat (Davis and Calabrese 1969) should be added. Phytoplankton smaller than the esophagus diameter of about 8 μ m should be considered. *Monochrysis lutheri* or *Isochrysis galbana* might be suitable. Larval food preference needs investigation.

After settlement and metamorphosis, juveniles seek a suitable permanent settling spot that will give them maximum protection. If juveniles are to be maintained in a particular area after settlement, a suitable substrate must be available to them, otherwise they will leave their original settling spot and be lost. For nonboring species a container with a sand bottom is adequate. For the boring species a spat collector that can give juveniles protection from as many angles as possible is preferred. Some nontoxic material with crevices or pits in it must be supplied for the boring species.

After they have settled, juveniles attached to spat collectors should be removed from the stagnant rearing system, which contains much decaying matter and benthic bacteria, and be transferred to a system that has a current of fresh seawater running through it. Juveniles should be raised to about 3–4 cm in length in the laboratory before they are introduced into the field to grow in natural ecosystems. Any size below this is very susceptible to predation. There is need for information on the survival of cultured juveniles that have been introduced back into the field to grow.

The animals probably show low growth rates

from day-2 to the acquisition of zooxanthellae because energy is being channeled for various developmental changes, such as the change in form of the prodissoconch shell, leaving less available for growth in shell length. Increased growth rates after the acquisition of zooxanthellae are probably brought about in a large part by the zooxanthellae themselves, which, according to Goreau, Goreau, and Yonge (1973), supply *T. maxima* with energy from photosynthetates and by digestion of older algal cells. The decrease in shell length of *T. maxima* at day 91 (Figure 7) occurs because the sample used contained smaller sized clams. Growth rates should be understood in the light of the limited nutrients available.

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LITERATURE CITED

- D'ASARO, C. N. 1967. The morphology of larval and postlarval *Chione cancellata* Linné (Eulamellibranchia: Veneridae) reared in the laboratory. *Bull. Mar. Sci.* 17(4): 949–972.
- DAVIS, H. C., and A. CALABRESE. 1969. Survival and growth of larvae of the European oyster (*Ostrea edulis* L.) at different temperatures. *Biol. Bull. (Woods Hole, Mass.)* 136(2): 193–199.
- GALTSOFF, P. S. 1938. Physiology of reproduction of *Ostrea virginica*. II. Stimulation of spawning in the female oyster. *Biol. Bull. (Woods Hole, Mass.)* 75: 286–307.

- GOREAU, T. F., N. I. GOREAU, and C. M. YONGE. 1973. On the utilization of photo-synthetic products from zooxanthellae and of a dissolved amino acid in *Tridacna maxima* f. *elongata* (Mollusca: Bivalvia). J. Zool. 169: 417-454.
- LABARBERA, M. 1974. Calcification of the first larval shell of *Tridacna squamosa* (Tridacnidae: Bivalvia). Mar. Biol. 25: 233-238.
- . 1975. Larval and post-larval development of the giant clams *Tridacna maxima* (Röding) and *Tridacna squamosa* Lamarck (Tridacnidae: Bivalvia). Malacologia 15 (1): 69-79.
- LOOSANOFF, V. L., and H. C. DAVIS. 1963. Rearing of bivalve molluscs. Pages 1-136 in F. S. Russell, ed. Advances in marine biology. Vol. 1. Academic Press, New York.
- RAVEN, C. P. 1958. Morphogenesis: the analysis of molluscan development. Pergamon Press, New York. 309 pp.
- STEPHENSON, A. 1934. The breeding of reef animals. 2. Invertebrates other than corals. Sci. Rep. Great Barrier Reef Exped. 3(9): 247-272.
- WADA, S. K. 1942. Notes on the tridacnid clams in Palau [in Japanese]. Kagaku Nanyo 5(1): 62-69.
- . 1952. Protandric functional hermaphroditism in tridacnid clams. Oceanogr. Mag. 4(1): 23-30.
- . 1954. Spawning in the tridacnid clams. Jpn. J. Zool. 11: 273-285.